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EVOLUTION OF OVIPOSITION HABITS IN *APHODIUS* DUNG BEETLES (COLEOPTERA: SCARABAEIDAE)

NOBUYO YOSHIDA AND HARUO KATAKURA
Zoological Institute, Faculty of Science, Hokkaido University,
Sapporo, 060, Japan

Abstract.—Oviposition habits of nine species of *Aphodius* dung beetles common in Sapporo, Hokkaido, northern Japan, were studied under laboratory conditions using glass cages supplied with soil and fresh cattle dung. Four types of oviposition habits were recognized. Type I: Eggs were laid singly in the dung on the ground. Type II: Eggs were laid singly in the soil beneath the dung. Type III: Each egg was laid in a small dung mass stuffed in a shallow burrow excavated beneath the dung. Type IV: Each egg was laid in the soil near the terminal end of a sausage-shaped dung mass buried beneath the dung. Although Types III and IV were similar in that females provided food for larvae, behavioral sequences of oviposition and provisioning were distinctly different between the two types. In Type III, an egg was laid after a dung mass was provided; whereas, in Type IV, an egg was laid before a dung mass was buried. Provisioning habits of Type III and Type IV seemed to have evolved independently from more primitive Types I or II, and from Type II, respectively. Oviposition habits of *Aphodius* were compared with those of two major groups of scarabaeid dung beetles, Geotrupinae and Scarabaeinae. Our Type III oviposition habit is analogous to those of certain species of Geotrupinae and Scarabaeinae, and Type IV to some Geotrupinae, indicating parallel evolution of dung burying habits in several lines of scarabaeid beetles.

Key Words.—Insecta, Scarabaeidae, *Aphodius,* dung beetles, oviposition, behavioral sequence, evolution

Reproductive biology of dung beetles belonging to the subfamily Aphodiinae has had little attention until recently, in spite of their dominance in the number of species and individuals in the north temperate zone (Balthasar 1964). Scattered records show that oviposition habits of Aphodiinae are diverse. Many species lay eggs directly in dung on the soil surface, or in the soil beneath the dung (Hafez 1939, White 1960, Landin 1961, Hanski 1980). A few species bury dung masses for larval food in the soil under droppings (Paik 1968; Hosogi et al. 1979, 1980). Obligatory or facultative kleptoparasitic species are also known (Hammond 1976 [and the references therein], Klemperer 1980, Kiuchi 1987).

Due to this diversity, the Aphodiinae may offer invaluable information for studying evolutionary origin of more elaborated oviposition habits found in two major groups of dung beetles: Geotrupinae and Scarabaeinae (for reviews, Halffter & Matthews 1966, Halffter & Edmonds 1982, Doube 1990). Unfortunately, however, oviposition habits of Aphodiinae species have not been studied in detail, except for a few species such as *Aphodius rufipes* (L.) (Madle 1934, Holter 1979, Klemperer 1980). For many species, only the scattered descriptions of egg site and/or larval feeding sites were available. Furthermore, there have been no quantitative studies specifically dealing with oviposition behavior or evolutionary trends in Aphodinae species.

In this paper, we will examine four types of oviposition habits distinguished for nine Japanese species (all belonging to *Aphodius*) on the basis of the results obtained by rearing under laboratory conditions.

Table 1. Types of oviposition habits and egg distributions of nine *Aphodius* species together with their reproductive periods and female body size. S: desiccated dung surface, U: moist upper half layer of dung, L: moist lower half layer of dung, M: margin between dung and soil, G: soil under dung.

Type	Species	*n*	% of eggs laid in					Total[a]	Repro-duction[b]	Body size[c] (mm)
			S	U	L	M	G			
I	*A. brachysomus*	23[d]	1.2	76.1	22.2	0.4	0.0	1417	spring	7.8 ± 0.58
I	*A. haemor-rhoidalis*	35[e]	4.4	26.5	38.9	23.0	7.1	113	spring	4.7 ± 0.23
I	*A. breviusculus*	18[e]	16.7	40.3	37.5	5.6	0.0	72	spring	4.6 ± 0.34
I	*A. pratensis*	22[e]	11.4	48.6	37.1	2.9	0.0	35	autumn	4.6 ± 0.31
II	*A. sordidus*	28[e]	0.0	0.0	0.0	0.0	100.0	70	autumn	6.5 ± 0.43
II	*A. rectus*	59[e]	0.0	0.0	4.9	7.6	87.6	185	spring	5.8 ± 0.42
II	*A. pusillus*	38[e]	0.0	2.8	8.3	11.1	77.8	36	spring	3.7 ± 0.28
III	*A. elegans*	45[d]	0.0	0.0	0.0	0.0	100.0	1576	autumn	11.6 ± 0.92
IV	*A. haroldianus*	48[d]	0.0	0.0	0.0	0.0	100.0	329	spring	9.4 ± 0.81

[a] Total number of eggs laid in all glass cages.
[b] Reproductive period (all species are univoltine in Japan).
[c] Female body length (mean ± SD, $n > 30$).
[d] Number of females separately reared.
[e] Number of adults reared (sex unknown).

Materials and Methods

The nine *Aphodius* species listed in Table 1 were reared. Each species was collected, at the peak of reproductive activity (Yoshida & Katakura 1985), from cattle dung at pastures in Hokkaido Agricultural Experiment Station (42°59′ N, 141°24′ E) in Sapporo, northern Japan, approximately 10 km from the laboratory of Hokkaido University, where the rearing was performed.

Of these species, *A. haroldianus* Balthasar and *A. elegans* Allibert have been known to bury dung and lay eggs near (*A. haroldianus*) or in (*A. elegans*) the buried dung masses (Paik 1968; Hosogi et al. 1979, 1980). Other species are considered to lay eggs directly in droppings on the ground, or in the soil under the droppings (Yoshida & Katakura 1985; M. Kiuchi, personal communication).

Beetles were reared in glass cages consisting of two vertical glass plates and a narrow wood frame, which formed the bottom and the two sides of the cage. One of the glass plates was fixed to the wood frame, but the other plate was removable permitting food changes and periodical inspections. The lower half of the cage was filled with humid sand, and then fresh cattle dung was placed on sand to a depth equal to one-quarter volume of the cage. The top of each cage was sealed with cotton cloth and 3 mm mesh nylon net to prevent escape of beetles. Several rearing cages were placed together in a wood box and were shaded by black sheets so as to keep them dark except for the top. Two sizes of glass cages were used according to the body size of beetle species (length × width × height: large cage, 19.0 × 1.4 × 25.0 cm; small cage, 12.5 × 0.6 × 10.0 cm).

The females collected at the peak of reproductive activity were assumed mated prior to collection (Yoshida & Katakura 1985). Then, a female of each of the three larger species (*A. elegans, A. haroldianus* and *A. brachysomus* Solsky, which were easily sexed) was released separately and individually into large glass cages. The other six species were difficult to sex externally, and so one to four adults (unknown sex) per small cage, or five to ten adults (unknown sex) per large cage, were released.

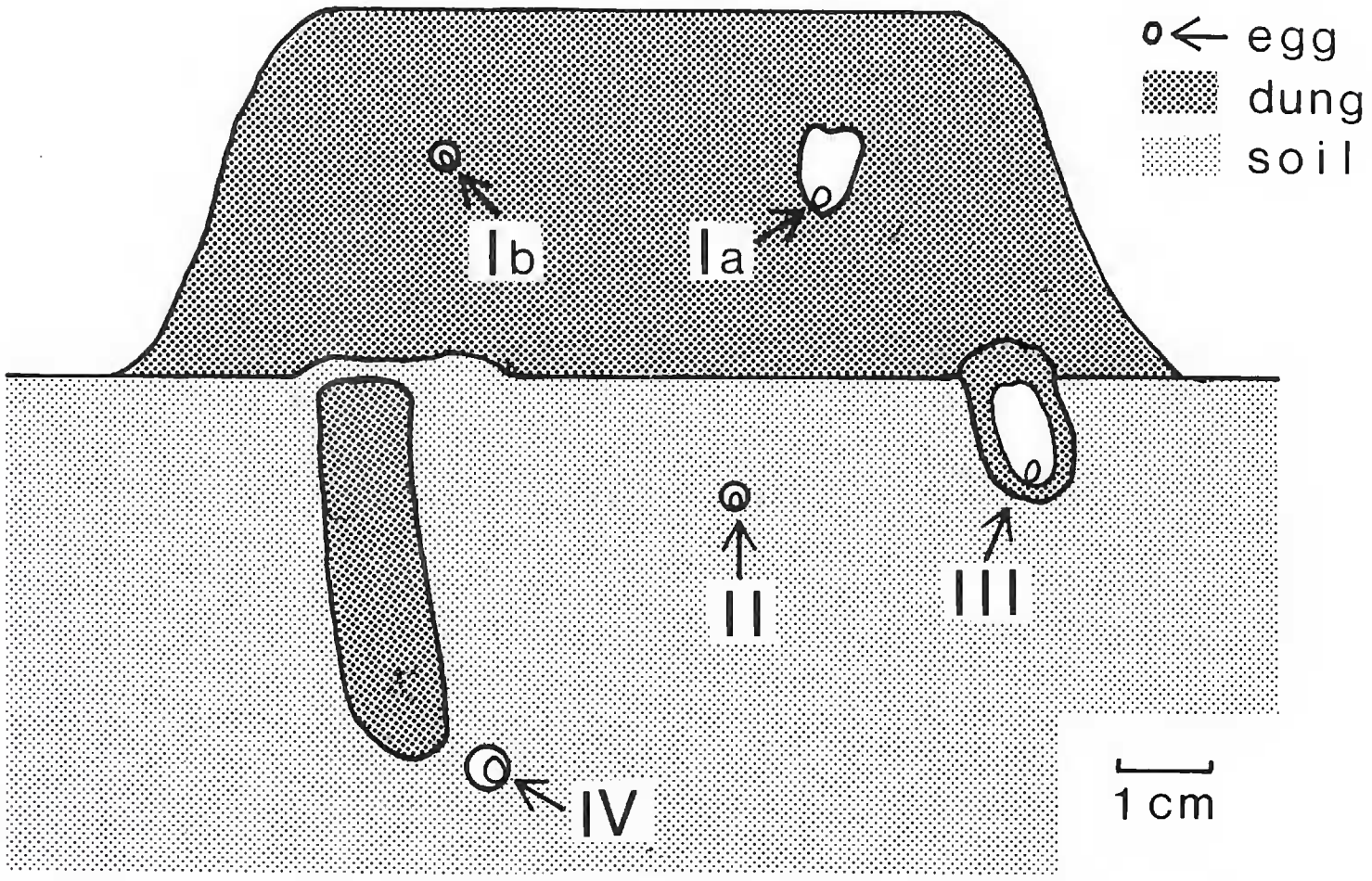

Figure 1. A scheme of oviposition sites of four types of oviposition habits distinguished for nine *Aphodius* species. I–IV: type of oviposition habits defined in the text; Ia, *A. brachysomus*; Ib, *A. haemorrhoidalis, A. breviusculus, A. pratensis.*

The dung and soil in each cage were changed every two or three days, after they were thoroughly examined to detect the oviposition sites and the number of laid eggs. In addition, position of laid eggs was traced, when necessary, on the transparent Saran Wrap®, which was placed on the glass plate. For the two species that bury dung for larvae, the dung burying process was also observed through the glass plate.

Species that reproduce in the spring (Table 1) were reared under long day conditions (LD 16:8) at 15 ± 1° C or 18 ± 1° C, and species that reproduce in the autumn were reared under short day conditions (LD 12:12) at 18 ± 1° C or 23 ± 1° C.

Results

Oviposition habits of the nine *Aphodius* species were classified into four types according to egg sites and presence or absence of provisioning for larvae (Table 1, Fig. 1).

Type I.—Four species were classified as Type I: *A. brachysomus, A. haemorrhoidalis* (L.), *A. breviusculus* (Motschulsky), *A. pratensis* Nomura & Nakane. Eggs were laid singly in round or oval spaces in the dung on the soil surface (Fig. 1, Ia, Ib).

The following is a summary of oviposition habits of *A. brachysomus,* the most intensively studied species of this type: Most eggs were laid in the middle part of cattle dung placed in the rearing cages (Table 1). Almost all eggs were laid in oval spaces (98.3%, $n = 1264$); the remainder were laid directly on the surface of tunnels left behind by the adults' passage. These spaces (Fig. 1, Ia) are probably egg chambers prepared by the mother beetles for oviposition. The spaces were

relatively large (6.7 ± 1.16 mm long, 4.4 ± 0.66 mm wide; mean ± SD, $n = 47$) and their inner wall was smooth, except for one side that was rough and protruded somewhat inwards into the space. No such space had more than one egg. Each egg was stood on end at the side opposite to the rough side of the space. It seems that the mother beetle makes an egg chamber, lays an egg, and closes it with rough dung fragments.

Eggs of the remaining three species of this type were also found singly in round or oval spaces, 1.3–2.4 mm diameter, inside of the dung (Fig. 1, Ib; Table 1). Whether these spaces were specially prepared egg chambers or mere spaces left behind by the adults' movement was not determined for these smaller species.

Type II.—Three species were classified as Type II: *A. sordidus* (Fabr.), *A. rectus* (Motschulsky), *A. pusillus* (Herbst). Eggs were laid singly in spaces in the soil beneath dung (Table 1; Fig. 1, II).

The spaces were simple and round, 1.5–3.0 mm diameter and not coated with dung. Because these spaces were apart from tunnels that were left behind by the adults' passage, they were probably specially prepared egg chambers. Most of the eggs were deposited at a depth shallower than 30 mm as follows: *A. sordidus,* 13.5 ± 11.28 mm; *A. rectus,* 11.1 ± 10.14 mm; *A. pusillus,* 10.3 ± 9.73 mm. Some eggs of *A. rectus* and *A. pusillus* were laid at the boundary between dung and soil, and a few others were in the lowest part of dung.

Type III.—One species was classified as Type III: *A. elegans.* Each egg was laid in a small dung mass stuffed into a shallow burrow in the soil beneath the dung (Fig. 1, III).

Dung masses were found shallower than 30 mm deep, and its top usually connected with the bottom of the above dung. The periphery of buried dung masses was mixed with grains of soil. Dung masses were 17.3 ± 3.6 mm long and 9.6 ± 1.6 mm wide ($n = 83$). There was a space in each mass, in which a single egg was usually laid (97.0% of masses with one egg, 0.4% with two eggs, and 2.6% with no egg, $n = 533$). The space (egg chamber) was 10.5 ± 2.79 mm long and 5.9 ± 1.37 mm wide ($n = 45$). The inner surface of the egg chamber was smooth at the bottom and sides, but rough at the top, sometimes protruding inwards. The dung wall was thin at the bottom (1.7 ± 1.41 mm) and sides (2.6 ± 0.92 mm) but thick at the top (4.4 ± 1.85 mm). Most eggs were laid on the lower one-half of the wall of egg chambers (58.5% of laid eggs; $n = 94$) or on the bottom (36.6%). Sometimes a few dung masses were fused together at their sides.

In the provisioning and oviposition processes, a female excavated a shallow burrow in the ground beneath dung, carried dung fragments from above, and plastered the wall of the burrow with dung so as to form a chamber. Although we could not trace subsequent processes, the female must smooth the inner surface, lay an egg and close it from above with dung fragments, judging from the condition of buried egg masses.

Type IV.—One species was classified as Type IV: *A. haroldianus.* Each egg was laid in the soil beneath the dung; after oviposition, the parental females buried a dung mass near the egg (Fig. 1, IV).

Buried dung masses were found in the soil up to 8 cm deep. They were similar to a sausage and often somewhat curved; 34.8 ± 8.4 mm long and 14.3 ± 3.2 mm wide ($n = 106$). Dung sausages were made of stratified compact dung and had no spaces within them. An egg was laid in a space in the soil 5–8 mm apart from the terminal end of each dung sausage. The space was on the average 6.6

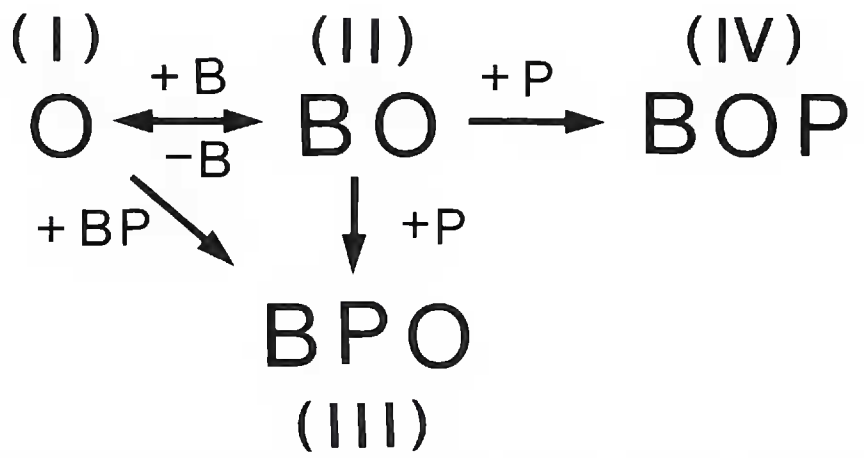

Figure 2. Suggested evolutionary relationships among four types of oviposition habits in *Aphodius*. I–IV: type of oviposition habits, O: oviposition, B: burrowing soil, P: provisioning dung into burrow.

mm long, 4.0 mm wide, and without any coating. Two or three masses sometimes fused together at the sides or at the terminal ends, at least in the narrow rearing cages.

In the provisioning and oviposition processes, a female excavated a vertical shaft beneath the dung and constructed an egg chamber near the end of the shaft. (Then, she probably lays one egg in the chamber and closes the chamber with soil, but these processes could not be confirmed in this study.) After oviposition, she filled the shaft with dung, mixed her own excrements with dung, and then she closed the shaft with soil. Sometimes, however, the dung sausage was not entirely buried but remained in contact with above unburied dung.

Discussion

Evolutionary Trends among Oviposition Habits.—Although it is yet uncertain which behavior type is most primitive among the four, Types I and II are evidently simpler and more primitive than Types III and IV. In Types III and IV, dung is supplied for the young, but the behavioral sequence of provisioning and oviposition is distinctly different between the two species. In Type III, a dung mass is first prepared in the soil, and then an egg is laid in the dung mass. On the other hand, in Type IV egg is laid in the soil before dung is buried to form a dung sausage. Because the sequence of oviposition and provisioning is thus inverted between the Types III and IV behaviors, it is likely that these two types evolved independently (Fig. 2).

Type IV behavior seems to have evolved from Type II; in both behaviors eggs are laid in the soil near (but not in) the larval food resource, and the behavioral sequence of oviposition habits in Type IV can be easily evolved from the simpler Type II, by adding provisioning behavior to the behavioral sequence of the latter (+P).

On the other hand, two alternative interpretations are possible for the evolution of Type III behavior: (1) this type may have evolved from Type II, by inserting provisioning behavior (P) between burrowing (B) and oviposition (O); or (2) Type III behavior may be introduced from Type I, by inserting burrowing and provisioning to the behavioral sequence of the latter (+BP). The first interpretation seems more parsimonious, but the second interpretation may be supported by the fact that in both Type III and Type I behaviors eggs are laid in the larval food resource.

Parallel Evolution of Dung Burying Habits.—Klemperer (1983) coined the term

"rummagers" for the *Aphodius* species that lay their eggs directly in droppings (synonymous with endocoprids sensu Hanski 1986, not sensu Bornemissza 1969), and contrasted them with "buriers" (paracoprids) that excavate burrows and fill them with dung masses in each of which an egg is laid, and with "rollers" (telocoprids) which roll away a ball of dung some distance before being buried in a chamber where the ball is either eaten or converted to a brood ball. According to this classification, species with Type I behavior are typical rummagers. Type II behavior species can also be called rummagers because their larvae freely feed on the dung on the soil surface, although they lay eggs outside of the dung.

On the other hand, species of Types III and IV behavior are buriers, in that both place dung in the soil for larvae. However, the prepared dung masses are small in behaviors of both Types III and IV, as described above. Larvae of species with Type III behavior cannot complete the growth with buried dung masses (second and third instars eat freely in droppings on the soil; Hosogi et al. 1979; NY, unpublished data). Larvae of species with Type IV behavior can complete the growth in the buried dung masses, but often depart from it and eat freely in unburied dung (third instars; NY, unpublished data). Accordingly, it seems more appropriate to treat behaviors of Types III and IV as intermediate states between rummagers and typical buriers completing growth only with buried dung masses.

Anyhow, behaviors of Types III and IV could be regarded as representing two basic types of oviposition habits found in buriers. Type III is analogous to the oviposition habits of many species of Scarabaeinae (e.g., the Oniticellini and Onthophagini; in particular, *Oniticellus egregius* Klug) and Geotrupinae (e.g., *Geotrupes spiniger* Marsham, *G. cavicollis* Bates) laying eggs in buried dung masses (Halffter et al. 1985, Klemperer 1979, Davis 1989). Type IV is essentially the same as the oviposition habits of some Geotrupinae, typically represented by *Typhoeus typhoeus* (L.) (Palmer 1978, Brussaard 1983) and *Ceratophyus hoffmannseggi* Fairmaire (Klemperer 1984), which lay each egg near the terminal end of a dung sausage buried in the soil.

Diversification of brood caring habits is prominent in two major groups of scarabaeid beetles, Scarabaeinae and Geotrupinae (Halffter & Matthews 1966, Halffter & Edmonds 1982). Almost all species of these two groups are presocial, and even in the most primitive type, adults provide foods for larvae. Ironically, this makes it difficult to seek the evolutionary origin of their presociality among these two groups of beetles. For the evolutionary origin of brood caring in dung beetles to be clarified, it is more preferable to concentrate our effort to the groups which include both species showing brood caring and those not. The present study showed that *Aphodius* beetles are particularly suitable for such purpose. We expect that closer ethological and ecological studies of *Aphodius* beetles will thus facilitate our unbiased understanding of the diverse brood caring habits evolved in coprophagous beetles of the family Scarabaeidae.

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